

Shade shelters increase survival and photosynthetic performance of oak transplants at abandoned fields in semi-arid climates

Claudia González-Salvatierra • Ernesto Iván Badano • Joel Flores • Juan Pablo Rodas

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Abstract: Forest restorations conducted in semiarid, seasonally dry climates must deal with the intense drought stress that affects tree seedlings during the dry season. Although this water deficit is the most commonly invoked source of mortality for seedlings, several other environmental factors may also preclude survival of transplants. For instance, it has been widely reported that excessive light reduces the efficiency of the photosynthetic apparatus, hence decreasing plant survival, but most seedling transplants in deforested areas are conducted under these light conditions. This study is focused in determining whether excessive light affects the photosynthetic performance and survival of *Quercus coccolobifolia*, a Mexican oak species, when their seedlings are transplanted in semiarid deforested areas. Further, this study tests the possibility of using artificial shade shelters to improve the ecophysiological performance and survival of seedlings. Oak seedlings were transplanted under full sunlight conditions and beneath artificial shade shelters of two different colors: white and black. To reduce water stress, and hence isolate the effects of light treatments, a drip irrigation system was implemented at each experimental plot. Seedling survival was monitored weekly for 128 days and photosynthetic performance was assessed by measuring chlorophyll fluorescence at three opportunities during the experiment. Sun-exposed seedlings showed lower photosynthetic performance and survival rates than those beneath shelters of both colors. These results suggest that sunlight damage can reduce seedling survival when they are transplanted in exposed sites, and that shade shelters can improve the success of forest restoration programs in semiarid climates.

Keywords: chlorophyll fluorescence; light stress; photoinhibition; reforestation; forest restoration

Introduction

Seedling establishment is a critical process for forest regeneration, but it can be affected by a number of abiotic variables. Precipitation and soil water retention, temperature and relative humidity, as well as the quantity and quality of light are the most commonly invoked factors affecting seedling establishment (Fenner and Thompson 2005). Despite the strong influence of these climatic factors on seedling establishment, most reforestation programs are still being conducted by directly transplanting large numbers of tree seedlings on large deforested areas in which extreme environmental conditions predominate (Sáenz-Romero 2003).

Under extreme environmental conditions, it has been suggested that the success of forest restoration programs may be increased by transplanting seedlings beneath nurse plants (Padilla and Pugnaire 2006). This strategy seems to perform well in semiarid and seasonally dry climates, when nurse plants ameliorate drought stress during the dry season and, hence, improve survival of transplants beneath their canopies (Castro et al. 2002; Gómez-Aparicio et al. 2004; Badano et al. 2009; Padilla and Pugnaire 2009). Indeed, some recent studies have shown that on sites where nurse plants are scarce, their beneficial effects on other species can be emulated by means of shade structures that also reduce the impact of water deficit on transplants (Badano et al. 2011). Nevertheless, besides water deficit, several other environmental variables might also preclude the success of transplants in semiarid climates.

Deforested areas in semiarid climates are commonly exposed to high solar radiation, and this can reduce the performance of tree seedlings used in restoration programs even when water availability is optimal (Badano et al. 2009). Although plants have a number of physiological pathways for dealing with excessive light, the recruitment of tree seedlings can ultimately be reduced if this stress factor is maintained over time. A primary photopro-

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Claudia González-Salvatierra • Ernesto Iván Badano (✉)
Joel Flores • Juan Pablo Rodas

División de Ciencias Ambientales, Instituto Potosino de Investigación Científica y Tecnológica, A.C., Camino a la Presa San José 2055, C.P. 78216, San Luis Potosí, S.L.P., México.

E-mail: ernesto.badano@ipicyt.edu.mx

Corresponding editor: Yu Lei

tection mechanism results from the reemission of excessive light to the environment as chlorophyll fluorescence. When plants are transferred from darkness into light, the reaction centers of photosystem II (PSII) are closed in order to protect the photosynthetic apparatus and, consequently, there is a peak of chlorophyll fluorescence at this moment. As plants adapt to light, chlorophyll fluorescence decreases due to increases in the rate at which the electrons are transported away from the PSII (Maxwell and Johnson 2000). Once plants are under steady illumination, fluorescence can rise again if the amount of light captured by chlorophylls surpasses the levels required for photochemistry (Govindjee 2004). Additionally, excess light energy can also be dissipated as heat by means of the xanthophyll cycle carotenoids, causing the non-photochemical quenching of chlorophyll fluorescence (Huner et al. 2008). If plants are unable to dissipate excess light energy by these pathways, then photoinhibition of photosynthesis may occur (Deming-Adams and Adams 2003). Photoinhibition is, therefore, a light-induced reaction that reduces the capacity of plants to convert light energy into dry material, hence decreasing plant growth and survival (Adams et al. 2008; Baker 2008; Takahashi and Murata 2008). Thus, besides water deficit, successful forest restoration in semiarid climates perhaps also requires dealing with the impacts of excessive light.

This study focused on this aim and assessed the impacts of excessive light on the survival and photosynthetic performance of *Quercus coccolobifolia*, a native oak species from central Mexico, when seedlings are transplanted at fully deforested areas in a semiarid climate. This species was chosen because the genus *Quercus* is one of the most charismatic components of the Mexican flora (Rzedowski 1966). However, oak forests have been intensively felled and their recovery is considered a priority for the country (Velásquez et al. 2002; Koleff et al. 2004). Additionally, since nurse plants do not typically occur in deforested areas of Mexico, this study proposes that the negative effects of excessive light can be ameliorated by protecting seedlings with artificial shade shelters.

Materials and methods

Study area and species description

This study was conducted on the western slopes of Sierra de Alvarez, state of San Luis Potosí (Mexico), within the communal farm *Monte Caldera* (22°11' N, 100°43' W, 2,100–2,300 m a.s.l.). The climate is semiarid with average annual air temperature of 16.8°C and mean annual precipitation of 304.5 mm. There is a markedly dry season between October and May, and up to 97% of rainfall events occur between June and September (García 1988). This site was originally covered by oak-dominated forests, but they were intensively felled during the last four centuries to provide fuelwood for the mineral smelters of local mines (Pedraza-Montes 1994). *Quercus coccolobifolia* Trel. (Fagaceae), belongs to the red oak group (section *Lobatae*). This is an endemic to Mexico that grows between 1,550 and 2,300 m a.s.l. (Valencia-Avalos 2004). Castillo-Lara et al. (2008) reported that

Q. coccolobifolia colonizes recently opened forest gaps in Sierra de Alvarez, suggesting that this is a pioneer species that contributes to forest regeneration after natural disturbances.

Experimental design

We conducted a field experiment to determine whether excessive light affects the survival and photosynthetic performance of *Q. coccolobifolia*, and whether these effects can be ameliorated by using shade shelters. Oak seedlings were transplanted to the study area in November 2010 after the rainy season. We chose this period for beginning the experiment because natural germination finishes at this time and oak seedling mortality increases monotonically as the dry season advances (Badano et al. 2009, 2011). Seedlings used in the experiment were grown from acorns collected from adult *Q. coccolobifolia* trees in Sierra de Alvarez. Acorns were individually sown in plastic bags (1,000 mL volume) filled with commercial peat and germinated in the greenhouse of Instituto de Zonas Desérticas, Universidad Autónoma de San Luis Potosí. All seedlings were 6-month-old (mean height = 10 cm) when taken to field. However, prior to transplanting, seedlings in bags were taken off the greenhouse for five days to pre-adapt them to environmental levels of light.

Transplants were performed by digging 45 circular holes (30 cm wide × 45 cm deep) arranged in three parallel lines (15 holes per line); all holes were spaced 1.5 m apart. After removing the plastic bags, two seedlings were transplanted at each hole and 600 mL of water were applied to reduce impact of handling. All seedlings were labeled and numbered. Immediately after transplanting, one of the following light treatments was randomly applied on each experimental plot: (1) shelters lined with white shade cloth; (2) shelters lined with black shade cloth; and (3) shelters without shade cloth (control), but lined with hexagonal wire mesh to protect seedlings from herbivores. By following this design, 30 seedlings were assigned to each light treatment. The physical support for the shelters was provided by table-like frames (0.4 m × 0.4 m × 0.6 m) constructed with 6 mm-diameter building iron. Greenhouse monofilament polyethylene 70% shade cloths (1 mm mesh size for both shade cloth colors; MallaPlas®, Mexico, D.F.) were used for lining the top and the sides of the shade shelters; therefore, shelters reduced the incoming light at all times of day (early morning, midday, and late afternoon). We used white and black shade cloths because it has been previously suggested that shade cloths of different colors differentially affect the physiological responses of oak seedlings because of differences in their light reflectance properties (Ashton and Berlyn 1994; Valladares et al. 2002; Ammer 2003).

To reduce water stress, and hence better isolate the effects of the light treatments, a drip irrigation system was installed on each experimental plot. Irrigation systems consisted of plastic bottles (600 mL in volume) with a small hole (3 mm) drilled in their caps. These bottles were filled with water and placed with the cap down in the soil, just to the side of each transplanted seedling. Bottles were refilled weekly to maintain the soil of the seedling root environment as near as possible to its field capacity.

Survival and photosynthetic performance of seedlings

Seedling survival was monitored weekly at each experimental plot for 128 days, from November 2010 (the beginning of the dry season) to April 2011 (the beginning of the rainy season). At each monitoring date, seedlings were considered dead if all their leaves were completely withered. However, since oak seedlings can drop their leaves in order to tolerate unfavorable environmental conditions (Fotelli et al. 2000), we assessed whether these seedlings resprouted on later dates in order to correct the previous records as necessary. During the experiment, dead seedlings were never replaced with new transplants.

To determine whether the shade shelters improved the photosynthetic performance of seedlings as compared with those in control plots, a portable pulse amplitude modulation fluorometer (Mini-PAM; H. Walz, Effeltrich, Germany) was used to measure a series of variables related to chlorophyll fluorescence (see below). Moreover, these variables were measured at three different times during the experiment to determine whether their variations concurred with seasonal changes in temperature and light intensity. The first round of measurements was conducted 24 days after beginning of the experiment, but not at day zero, in order to allow transplants time to stabilize in their new environment and, hence, avoid measuring the possible impacts of seedling manipulation (i.e., transplant stress). The second round of measurements was performed approximately at the middle of the experiment, on day 74, and the last measurements were at the end of the experiment, on day 128. Each time that chlorophyll fluorescence was measured, the external sensors integrated to the clamp of the Mini-PAM also recorded the leaf temperature (LT) and the photon flux density (PFD) within the experimental plots of the different light treatments.

Since mortality increased with time, chlorophyll fluorescence measurements were conducted on all surviving seedlings we recorded at each monitoring date. The first round of measures (day 24) included 15 seedlings beneath black shelters, 19 seedlings beneath white shelters and 14 seedlings in control plots. The second round of measurements (day 74) included 12 seedlings beneath black shelters, 13 seedlings beneath white shelters and 10 seedlings in control plots. The final round of measurements (day 128) included 11 seedlings beneath black shelters, 13 seedlings beneath white shelters and 7 seedlings in control plots. These measures were always conducted on a mature leaf of each seedling. Chlorophyll fluorescence was first measured at pre-dawn (between 5:00 and 6:00) on dark-adapted seedlings to assess the maximum quantum efficiency of photosystem II. This variable was estimated as:

$$\frac{F_m^0 - F_0}{F_m^0} = \frac{\Delta F}{F_m^0} \quad (1)$$

where, F_0 is the chlorophyll fluorescence emitted by the dark-adapted leaves and F_m^0 is the maximum fluorescence that chlorophylls emit when a saturating pulse of actinic light is ap-

plied (Maxwell and Johnson 2000). In most plant species, the values for this ratio oscillate between 0.80 and 0.83 if environmental stress is negligible, but lower values are observed as environmental stress increases (Maxwell and Johnson 2000).

Chlorophyll fluorescence was also measured at noon (between 13:00 and 14:00). We did this because, at this latitude, this is the moment of day when maximum sunlight incidence and, thus, the photoprotective effects of shade structures would be highest. Chlorophyll fluorescence data recorded at noon was used to estimate:

(1) The effective quantum yield of photosystem II, which was computed as:

$$\Phi_{PSII} = \frac{F_m' - F_t}{F_m'} \quad (2)$$

where F_t is the chlorophyll fluorescence under steady-state illumination (i.e., light conditions in the field) and F_m' is the maximum fluorescence emitted by chlorophylls when a saturating pulse of actinic light is superimposed to environmental levels of light (Genty et al. 1989).

(2) The non-photochemical quenching efficiency, calculated as:

$$NPQ = \frac{F_m^0 - F_m'}{F_m'} \quad (3)$$

(3) The electron transport rate, which was estimated as:

$$ETR = \Phi_{PSII} \times PFD \times 0.84 \times 0.5 \quad (4)$$

where, PFD is the photon flux density of the environmental light, and 0.84 and 0.5 are constants that account for the fraction of light absorbed by the photosynthetic tissue and the partitioning of light energy between the photosystems II and I, respectively (Ritchie and Bunthawin 2010). For performing all these measures, the saturating light pulse emitted by the Mini-PAM was calibrated to about 2,500 mol photon·m⁻²·s⁻¹. All these measures were conducted on full-sunny days and also included all surviving seedlings recorded at each experimental plot.

Statistical analysis

To determine whether light treatments affected seedling survival, the Kaplan-Meier method (Kaplan and Meier 1958) was used to construct a survival curve for each treatment. This method considers each seedling as a replicate and, thus, survival curves are estimated by using binary data sets that indicate whether each seedling was dead or alive on each monitoring date. Later, the generalized Gehan-Wilcoxon test was used to assess differences in survival rates among curves and, once significant differences were detected, the two-sample Cox-Mantel test was used to determine differences between pairs of treatments (Lee et al. 1975).

The values of LT , PFD , F/F_m^0 , Φ_{PSII} , NPQ and ETR were compared among light treatments and monitoring dates by using repeated measures ANOVAs. However, since the number of surviving seedlings decreased with time in all treatments, just seven seedlings per treatment were selected for these comparisons. We did this to standardize the number of replicates included in the repeated measures ANOVAs. These seedlings were selected by following two criteria: first, they must have been recorded alive on all monitoring dates; and, second, they cannot belong to the same experimental plot. The *post hoc* Tukey test was applied only when significant differences among treatments were detected. All statistical analyses described in this section were conducted with the software R 2.13 (R Development Core Team 2011).

Results

The survival of *Q. coccolobifolia* seedlings decreased with time in all light-manipulation treatments, showing an abrupt decline during the first 20 days of the experiment. After this date, the decline in survival was slower and survival curves stabilized after 100 days in all light treatments (Fig. 1). At the end of the experiment, seedling survival was 48% beneath white shelters, 37% beneath black shelters, and 23% at control plots exposed to sun (Fig. 1). Seedling survival rates differed significantly between light treatments (Gehan-Wilcoxon Chi-square = 7.109; $df = 2$; $p = 0.002$) and pairwise comparisons indicated that survival rates were higher beneath shade shelters than at control plots. Survival rates were, however, significantly higher beneath white shelters than beneath black ones (Cox-Mantel test $p < 0.001$ in all cases).

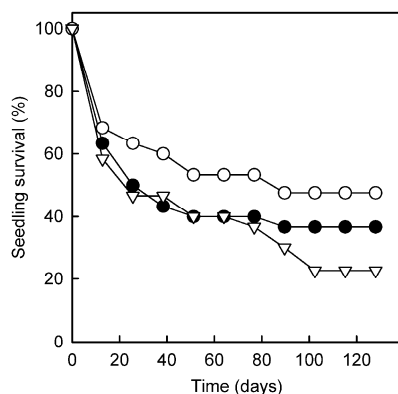


Fig. 1 Kaplan-Meier estimated survival curves for seedlings of *Q. coccolobifolia* transplanted beneath white-meshed shade shelters (empty circles), black-meshed shade shelters (solid circles), and at control plots exposed to sun (empty triangles).

Predawn LT values varied significantly between monitoring dates ($F_{(2,36)} = 887.652$, $p < 0.001$), but no effects were indicated for light treatments ($F_{(2,18)} = 1.012$, $p = 0.383$). The interaction between light treatments and monitoring dates did not affect the values of this variable ($F_{(4,36)} = 0.317$, $p = 0.865$). In all light

treatments, predawn LT values were below 8°C at the beginning and middle of the experiment, but surpassed 13°C on the last monitoring date (Fig. 2A). Similarly, LT values at noon differed between monitoring dates ($F_{(2,36)} = 1099.529$, $p < 0.001$), but neither light treatments ($F_{(2,18)} = 1.831$, $p = 0.188$) nor their interaction with monitoring dates ($F_{(4,36)} = 1.547$, $p = 0.209$) affected this variable. At noon, seedlings in all light treatments showed LT values below 23°C on the first monitoring date but, later, these LT values progressively increased until they surpassed 30°C on the last monitoring date (Fig. 2A).

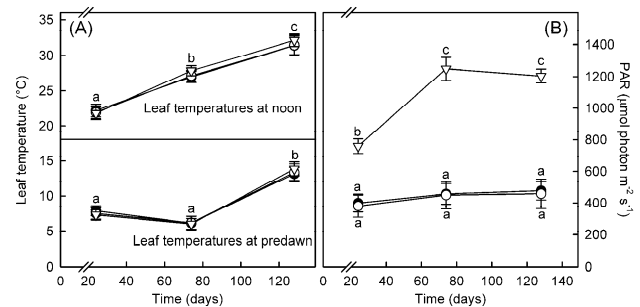


Fig. 2 Average values ($\pm 95\%$ confidence intervals; $n = 7$ for all light treatments) of (A) leaf temperature at predawn (lower panel) and at noon (upper panel), and (B) photosynthetically active radiation measured at the different monitoring dates beneath white shade shelters (empty circles), black shade shelters (solid circles), and at control plots (empty triangles). Significant differences between averages (Tukey test critical = 0.05) are indicated with different letters accompanying the symbols, or groups of symbols in the case of leaf temperatures.

The environmental PFD values taken at noon differed between monitoring dates ($F_{(2,36)} = 15.423$, $p < 0.001$) and light treatments ($F_{(2,18)} = 203.659$, $p < 0.001$). Indeed, there was also a significant effect of the interaction between treatments and time on this variable ($F_{(4,38)} = 4.168$, $p = 0.007$). The average PFD was lower beneath shade shelters than at control plots on all monitoring dates, and no differences were detected between shade cloth colors across monitoring dates (Fig. 2B). Conversely, environmental PFD at control plots increased from the first to the last monitoring dates (Fig. 2B).

The F/F_m^0 ratio differed significantly between light treatments ($F_{(2,18)} = 74.858$, $p < 0.001$) and monitoring dates ($F_{(2,36)} = 5.088$, $p = 0.011$), but no effects were indicated for interaction between these experimental factors ($F_{(4,36)} = 1.466$, $p = 0.232$). On all monitoring dates, seedlings transplanted beneath both white and black shelters showed higher F/F_m^0 ratios than seedlings transplanted to control plots (Fig. 3A). The Φ_{PSII} values, on the other hand, were affected significantly by light treatments ($F_{(2,18)} = 74.030$, $p < 0.001$), monitoring dates ($F_{(2,36)} = 5.381$, $p = 0.009$) and their interaction ($F_{(4,36)} = 3.250$, $p = 0.022$). Seedlings beneath shade shelters always showed higher Φ_{PSII} values than those at control plots, but no differences were detected between shelters of different colors across monitoring dates (Fig. 3B).

The NPQ differed between light treatments ($F_{(2,18)} = 36.026$, $p < 0.001$) and monitoring dates ($F_{(2,36)} = 80.563$, $p < 0.001$). This

variable was also affected by the interaction of these two factors ($F_{(4,36)} = 5.238$, $p = 0.002$). NPQ values increased from the first to the last monitoring date in all light treatments, but seedlings at control plots always showed significantly higher NPQ than those beneath the shade shelters (Fig. 3C). No differences in NPQ values were detected between seedlings transplanted beneath shade shelter of different colors (Fig. 3C).

The *ETR* of seedlings was also significantly affected by light treatments ($F_{(2,18)} = 15.554$, $p < 0.001$), monitoring dates ($F_{(2,36)} = 36.723$, $p < 0.001$) and their interaction ($F_{(4,36)} = 3.315$, $p = 0.021$). The lower *ETR* values were recorded on the first monitoring date and these values did not differ between light treatments (Fig. 3D). *ETR* values increased on the second monitoring date, but they were significantly higher for seedlings beneath shade shelters than those at control plots (Fig. 3D). At the end of the experiment, seedlings beneath white shelters displayed higher *ETR* values than those transplanted beneath black shelters or to control plots (Fig. 3D).

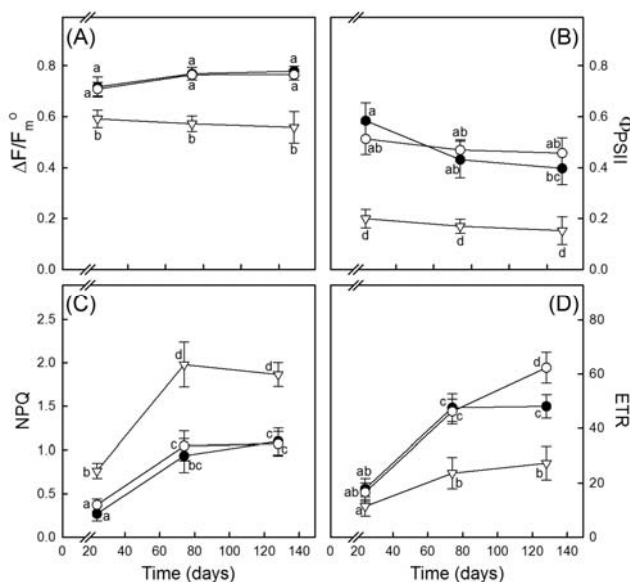


Fig. 3 Average values (\pm 95% confidence intervals; $n = 7$ for all light treatments) of (A) maximum quantum efficiency of photosystem II (F/F_m^0), (B) effective quantum yield of photosystem II (Φ_{PSII}), (C) non-photochemical quenching of chlorophyll fluorescence (NPQ), and (D) electron transport rate (ETR) measured at the different monitoring dates beneath white shade shelters (empty circles), black shade shelters (solid circles), and at control plots (empty triangles). Significant differences between averages (Tukey test critical = 0.05) are indicated with different letters accompanying the symbols.

Discussion

This study clearly demonstrates that the survival and physiological performance of *Q. coccolobifolia* seedlings transplanted in the field can be improved by using either white or black shelters (Fig. 1). Since shelters did not affect leaf temperature while strongly reducing PFD, as compared to sun exposed plots (Fig. 2), their positive effects on survival could be related to the ame-

lioration of the extreme sunlight conditions that seedlings face in the field. However, it is important to note that those seedlings transplanted beneath white shelters displayed higher survival rates than seedlings located beneath black shelters. Since shelters of both colors reduced light intensity to the same magnitude (Fig. 2), these differences in survival could be linked to different properties of white and black polyethylene fibers to reflect solar radiation. For instance, white polyethylene fibers have been reported to be more effective than black ones in reflecting both white light and ultraviolet rays (Benavides-Mendoza et al. 2000, 2002) and this, among other factors, may have caused the difference in survival. Nevertheless, since we were unable to measure these properties on the polyethylene cloths used in the experiment, these effects remain as hypotheses until more studies are conducted.

Artificial shade shelters also seem to reduce the negative impacts of excessive sunlight on the photosynthetic apparatus (Fig. 3). For instance, the maximum quantum efficiency of photosystem II in seedlings protected beneath shelters approached its expected optimum value ($F/F_m^0 \approx 0.8$; Maxwell & Johnson 2000). In contrast, these values were always below 0.6 for unshaded seedlings. This indicates that the photosynthetic apparatus of the oak seedlings transplanted under full sunlight conditions cannot recover during the night, and also suggests that photodamage to these seedlings is irreversible. Conversely, sheltered seedlings did not apparently suffer excessive photodamage during the day, and their photosynthetic apparatus recovered well during the night.

The effective quantum yield of photosystem II (Φ_{PSII}), on the other hand, was lower than the F/F_m^0 ratios in all light treatments. This decrease in the values of the ratio between variable and maximum fluorescence during the day is related to increases in the emission of fluorescence when chlorophylls are exposed to more light than can be handled by the electron transport chain in the thylakoid membrane (Duan et al. 2005; Guchou et al. 2007). However, seedlings directly exposed to sunlight always displayed lower Φ_{PSII} values, closer to zero, than seedlings transplanted beneath either white or black shelters. Therefore, this suggests that unprotected seedlings were exposed to intense physical stress, as compared to seedlings protected by shade shelters.

The protective effects of shade shelters were also reflected in lower values of non-photochemical quenching (NPQ). The NPQ values of seedlings that were transplanted to control plots were almost double those recorded on seedlings beneath shade shelters, especially at the middle and the end of the experiment (Fig. 3). This indicates that sun-exposed seedlings required dissipation of quantities of light energy in excess of those required for photochemistry or of those reemitted to the environment as fluorescence (Krause and Jahns 2004; Müller et al. 2001). Thus, this also suggests that unshaded seedlings would be more deeply affected by photoinhibition than those transplanted beneath shade shelters.

Electron transport rates (ETR) were also higher in seedlings protected with shade shelters than in those seedlings transplanted to control plots. Indeed, these differences in ETR between shel-

tered and unsheltered seedlings increased through the course of the experiment (Fig. 3). This may have occurred because individuals beneath shelters raised their *ETR*'s with time, while seedlings directly exposed to sunlight showed lower and constant *ETR* values during the course of the experiment. Because *ETR* is positive related to the ability of plants to assimilate CO₂ (Kitao et al. 2003), these results suggest that the photosynthetic performance of artificially shaded seedlings increased with time. If so, the use of shade shelters could increase both the survival and growth rates of seedlings used in reforestation.

As a final remark, this study clearly demonstrates that artificial shade shelters increased the survival of *Q. coccolobifolia* seedlings, a putative pioneer oak species from semiarid climates of central Mexico (Castillo-Lara et al. 2008). Indeed, the results of our field experiment showed that shade shelters decrease the impact of photoinhibitory processes and increase the survival rates of transplanted seedlings. Thus, although most studies conducted in semiarid climates concluded that drought stress is the main limiting factor for the establishment of tree seedlings in deforested areas (e.g.: Castro et al. 2002; Gómez-Aparicio et al. 2004; Badano et al. 2009; Padilla and Pugnaire 2009), our results suggests that excessive light may also reduce the success of these reforestations. However, it is important to recognize that this study leaves a number of open questions. How long must shade shelters be used to protect seedlings? What is the best cloth color for lining these shelters? Are other physiological pathways of seedlings, besides those related to light handling, affected by shade shelters? What tree species really require these shelters? The answers to all these questions would contribute to development of novel and better methodologies for forest restoration and reforestation in semiarid climates.

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